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Correspondence and requests for materials should be addressed to W.-H.L. (e-mail: [whli@uchicago.edu](mailto:whli@uchicago.edu)).

## Future projections for Mexican faunas under global climate change scenarios

A. Townsend Peterson\*, Miguel A. Ortega-Huerta†, Jeremy Bartley‡, Victor Sánchez-Cordero§, Jorge Soberón||, Robert H. Buddemeier‡ & David R. B. Stockwell¶

\* Natural History Museum; † Department of Geography and Kansas Applied Remote Sensing Program; ‡ Kansas Geological Survey and Department of Geography, The University of Kansas, Lawrence, Kansas 66045, USA  
 § Departamento de Zoología, Instituto de Biología, Apartado Postal 70-153; || Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, D.F. 04510, México  
 ¶ San Diego Supercomputer Center, University of California, 9500 Gilman Drive, La Jolla, California 92093, USA

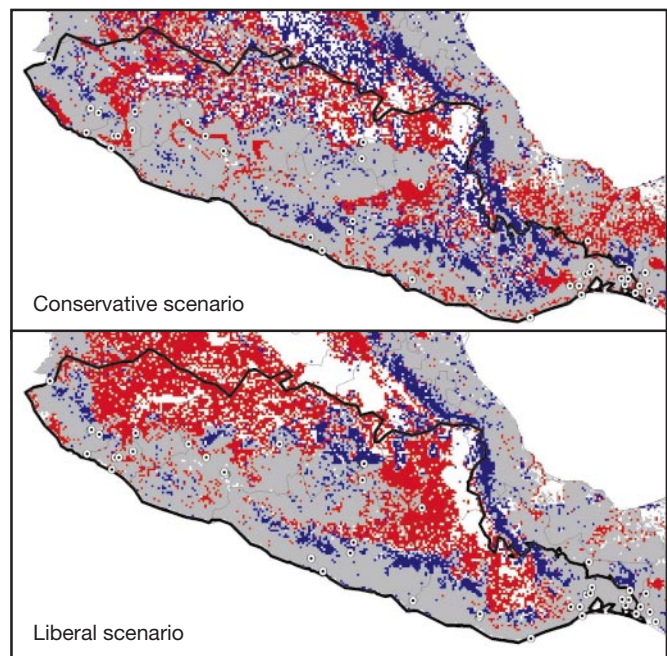
Global climates are changing rapidly, with unexpected consequences<sup>1</sup>. Because elements of biodiversity respond intimately to climate as an important driving force of distributional limitation<sup>2</sup>, distributional shifts and biodiversity losses are expected<sup>3,4</sup>. Nevertheless, in spite of modelling efforts focused on single species<sup>2</sup> or entire ecosystems<sup>5</sup>, a few preliminary surveys of fauna-wide effects<sup>6,7</sup>, and evidence of climate change-mediated shifts in several species<sup>8,9</sup>, the likely effects of climate change on species' distributions remain little known, and fauna-wide or community-level effects are almost completely unexplored<sup>6</sup>. Here, using a genetic algorithm and museum specimen occurrence data, we develop ecological niche models for 1,870 species occurring in Mexico and project them onto two climate surfaces modelled for 2055. Although extinctions and drastic range reductions are predicted to be relatively few, species turnover in some local communities is predicted to be high (>40% of species), suggesting that severe ecological perturbations may result.

We present a fauna-wide suite of predictions of the biodiversity consequences of global climate change. Taking advantage of the enormous biodiversity data resources accumulated by Mexico's Comisión para el Conocimiento y Uso de la Biodiversidad (CONABIO), as well as new tools in biodiversity informatics and quantitative geography<sup>10</sup>, we develop predictions of the effects of global climate change on distributions of 1,870 species (all 1,179 birds, all 416 mammals and all 175 butterflies of the families Papilionidae and Pieridae in Mexico) under two scenarios of global climate change (one conservative, one liberal) and three assump-

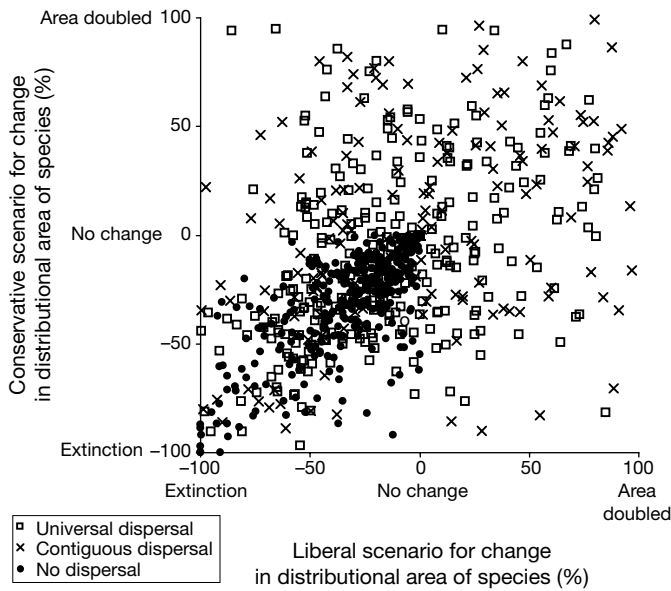
tions about dispersal ability<sup>11</sup>. We use the Genetic Algorithm for Rule-set Prediction (GARP), a machine-learning system that has shown excellent predictive ability in delineating species' ecological niches and predicting geographic distributions<sup>12</sup>. This first large-scale application of species-by-species models to the challenge of understanding the biodiversity consequences of global climate change provides a first view of the consequences of climate-change processes across a biodiversity-rich region.

To provide a detailed example of model results for a species, we examine the distribution of the west Mexican chachalaca (*Ortalis poliocephala*), a bird species endemic to tropical southwestern Mexico. Its present geographic distribution was summarized well by the ecological niche model, with correct prediction of 90% of independent test points, indicating that the model of the species' ecological niche was adequate. Under both scenarios of climate change, although the coastal portion of the species' distribution remained intact, the interior portion became less habitable, and a narrow band in the foothills of the coastal mountain ranges (Sierra Madre del Sur) more habitable (Fig. 1). Assuming universal dispersal abilities (not a good assumption), the species would encounter overall somewhat less (22.7% decline under the conservative climate change scenario) or more (75.1% increase under the liberal scenario) habitable area. However, under more realistic limited dispersal assumptions (dispersal into contiguous areas or no dispersal), the two scenarios agree more closely (conservative scenario 33.7% decrease, liberal scenario 29.7% decrease).

Examining patterns of change in distributional area across all 1,870 species, two climate-change scenarios, and three distributional assumptions analysed, consistent patterns emerge: species'



**Figure 1** Example of analyses of effects of global climate change on a species' (*Ortalis poliocephala*) potential geographic distribution. Top, changes expected under the conservative scenario of the Hadley simulation; bottom, changes expected under the liberal scenario. Grey areas indicate conditions appropriate for the species both at present and under the scenario of change; white areas indicate conditions inappropriate for the species both at present and under the scenario of change; red areas are at present appropriate, but are predicted to become uninhabitable by the species; blue areas are at present not appropriate, but are predicted to become appropriate for the species; dotted circles represent known occurrence points; the black line indicates present geographic limits to species' distribution. Areas outside the black line correspond to the distributions of other *Ortalis* species, and represent areas of overprediction owing to historical factors<sup>21</sup>.



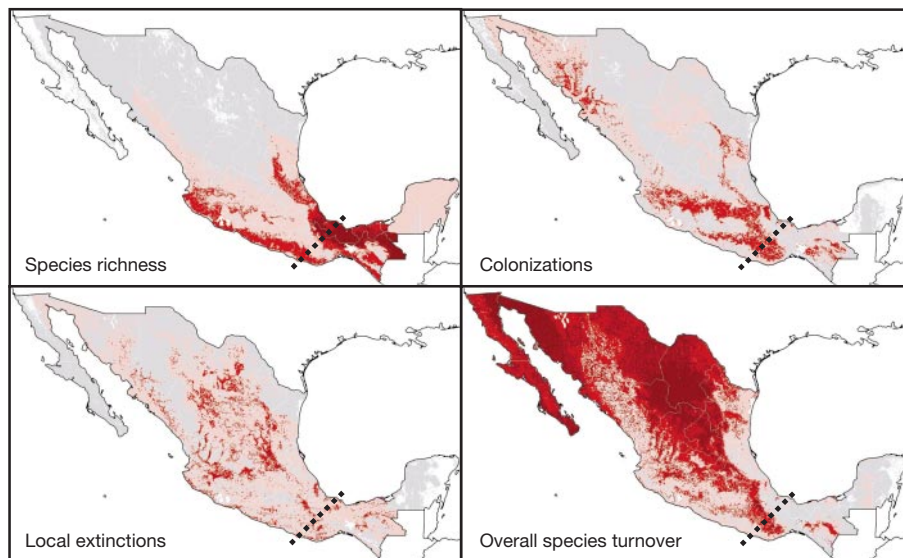
**Figure 2** Distribution of expected percentage change in distributional area of 334 species endemic to Mexico under two scenarios of climate change (conservative and liberal) and three scenarios of dispersal abilities (universal, contiguous and no dispersal). -100%, extinction; 0%, no change; 100%, doubling of distributional area.

distributions expand and contract with equal frequency under the universal dispersal ability assumption, but show increasing tendencies to contract under the contiguous dispersal and no dispersal assumptions. To estimate the magnitude of distributional area changes to be expected without the biases introduced by political boundaries, we focused on 334 species endemic to Mexico (Fig. 2), none of which is predicted to expand its range outside of Mexico. Under the unrealistic assumption of universal dispersal ability, the species' distributional area expand and contract with equal frequency; results are similar under the contiguous dispersal assump-

tion. Under the assumption of no dispersal ability, however, almost all species decline, and numbers of species suffering extreme reductions in distributional area (90% or more) are higher (2.4% of species). Reduction of distributional area is a consistently good predictor of species extinction, so these numbers represent minimum estimates of species in grave danger of extinction under these scenarios<sup>13</sup>: 0–2.4% of species are predicted to lose  $\geq 90\%$  of the present distributional area, and 5.1–19.5% are predicted to lose  $\geq 50\%$  of the present distributional area, under the three dispersal assumptions. The two climate-change scenarios are similar in the qualitative patterns predicted, although the liberal scenario predicts more dramatic effects in 11% of species (Fig. 2). No significant differences exist between taxonomic groups (mammals, birds, butterflies) in expected severity of effects on species' distributional areas; however, the butterfly families treated herein have relatively good dispersal abilities, and thus may not differ much from birds in this regard.

Gain and loss of species is distributed unevenly across Mexico (Fig. 3). Under the assumption of dispersal only into contiguous areas (averaging across the two climate-change scenarios), colonizations concentrate along the major sierras of Mexico, whereas extinctions are focused in the broad, open Chihuahuan desert and northwestern coastal plain. When we sum colonizations and extinctions for each grid cell (averaging between climate-change scenarios) across all species, and relate them to present species richness as a measure of species turnover, foci of turnover are evident in northern Mexico in the Chihuahuan desert, in interior valleys extending south to Oaxaca, and in the Baja California peninsula (predicted turnover rates as high as 45%). Because of the general northward trend of species' distributional shifts, and in view of the complicating effects of political boundaries, the southern quarter of the maps in Fig. 3 should be interpreted with caution: species moving into Mexico from the south, or incompletely modelled owing to Central American populations being excluded from our modelling efforts, may change the results.

The analyses presented herein illustrate the magnitude of effects that may be expected as a consequence of global climate change. Although only limited numbers of species will face entirely unsuit-



**Figure 3** Modelled species turnover in biological communities (1,870 species) across Mexico. Modelled current species richness: white, <155 species; grey, 155–306 species; pink, 307–458 species; red, 459–610 species; dark red, 611–763 species. Local extirpations: white, <29 species; grey, 29–56 species; pink, 57–84 species; red, 85–112 species; dark red, 113–140 species. Colonizations: white, <25 species; grey,

25–48 species; pink, 49–71 species; red, 72–95 species; dark red, 96–119 species. Species turnover: white, <10%; grey, 10–20%; pink, 20–30%; red, 30–40%; dark red, >40. The southern quarter of these maps (indicated by dashed line), however, may be subject to some bias (see text), and thus should be interpreted with caution.

able conditions for persistence, others will experience drastic reductions and fragmentation of distributional areas, or extend their distributions, creating new natural communities with unknown properties. Indeed, some workers<sup>14</sup> have argued that these reorganizations of communities will produce stronger distributional effects than will the direct effects of climate change on species' distributions; in this sense, our models provide null hypotheses of distributional expectations in the absence of strong interaction effects. More generally, these approaches to modelling distributional change caused by global climate change can be used to produce synthetic models of the combined effects of climate change and other scenarios (for example, species' invasions<sup>15</sup>), allowing us to address questions of productivity in economically important ecosystems, emerging diseases and other complex challenges<sup>16</sup>. □

## Methods

The general approach to modelling climate change effects on biodiversity is developed in detail elsewhere<sup>11</sup>, as are the details of the algorithm used for modelling species' ecological niches<sup>17,18</sup>.

## Data on distributions and ecological dimensions

Distributional data representing 112,456 records (that is, unique species × latitude–longitude combinations) for all 1,179 bird species in Mexico (a revised taxonomic treatment<sup>19</sup>; migrants and residents included), all 416 mammal species in Mexico, and 175 butterfly species (all the Papilionidae and Pieridae in Mexico) were obtained from continuing efforts to assemble distributional information on Mexican species from natural history museums around the world by the Comisión Nacional para el Uso y Conocimiento de la Biodiversidad (CONABIO; <http://www.conabio.gob.mx/>). Forty-five museums<sup>20–22</sup> contributed data. Environmental data were provided on a 4 × 4 km grid by CONABIO (annual mean temperature in 15 classes, annual mean precipitation in 19 classes) and the Defense Mapping Agency (digital elevation model; <http://edcdaac.usgs.gov/gtopo30/hydro/namerica.html>). From the latter, coverages summarizing elevation, slope, aspect and potential solar radiation (all continuous) were extracted. The categorical temperature and precipitation maps were converted into pseudo-continuous maps using pycnophylactic interpolation, a mass-preserving spatial interpolation for categorical data<sup>23</sup>.

## Scenarios of climate change

The general circulation model used<sup>24</sup> (HadCM2) includes several scenarios. We assessed both a conservative and a less conservative view of how climates could change over the next 50 years using the HHGSDX50 and HHGGAX50 scenarios ([http://ipcc-ddc.cru.uea.ac.uk/cru\\_data/examine/HadCM2\\_info.html](http://ipcc-ddc.cru.uea.ac.uk/cru_data/examine/HadCM2_info.html)). The HHGSDX50 scenario assumes an increase of 0.5% CO<sub>2</sub> per year (IS92d), and incorporates sulphate aerosol forcing, making it a relatively conservative estimate of climate change. The HHGGAX50 scenario assumes a 1% increase of CO<sub>2</sub> per year (IS92a), and does not allow for the effects of sulphate aerosols, and so is more liberal. Results are based on a 30-year average around 2055 (2040–2069); our models therefore do not take into account potential effects of increased climate variability (El Niño events, in particular) on species' distributions. Data are provided at a spatial resolution of 2.5° × 3.75°. Expected changes in temperature (°C) and precipitation (mm) under each scenario were extracted; to increase resolution, we interpolated to 0.5 × 0.5° cells using a nearest-neighbour contouring algorithm, as suggested in the data guidelines of the Intergovernmental Panel on Climate Change (<http://ipcc-ddc.cru.uea.ac.uk/>). These coverages of expected change were used to increment the pseudo-continuous current temperature and precipitation maps. The resulting estimated climate (annual averages) coverages of Mexico for the mid-twenty-first century indicate that the average annual mean temperature of Mexico may increase by 1.6–2.5°, and mean annual precipitation may decrease by 70–130 mm. Although inclusion of intermediate time-slice scenarios in such modelling efforts would be greatly desirable, in the present example, it is not necessary, as shifts in species' distributions were relatively subtle.

## Ecological niche modelling and dispersal assumptions

The ecological niche of a species can be defined as the conjunction of ecological conditions within which it can maintain populations without immigration<sup>25,26</sup>; as such, it is defined in multidimensional ecological/environmental space<sup>27</sup>. Several approaches have been used to approximate species' ecological niches<sup>28</sup>; of these, the most robust appears to be the genetic algorithm for rule-set prediction (GARP), which includes several inferential approaches in an iterative, artificial-intelligence-based approach<sup>17</sup>, and has had extensive testing<sup>12,17,29</sup>. GARP works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection to produce a heterogeneous (for example, logistic regression, bioclimatic rules) rule set describing the species' ecological niche.

Ecological niche models developed with GARP can be projected onto current and modelled future landscapes. Projection onto the current landscape indicates present-day geographic distribution of suitable conditions. Because species' distributions are limited by both ecological and historical factors (such as barriers to dispersal)<sup>21</sup>, we restricted predicted distributions to those ecoregions (<http://www.conabio.gob.mx/sig/>

acera\_sig\_pr.html) in which the species had actually been recorded<sup>11</sup>. GARP models can also be applied to climate-change-transformed landscapes to identify areas of potential distribution for a species after modelled environmental changes.

We synthesized pre-change maps and liberal and conservative post-change maps (averaged for extinction calculations) for each species by measuring potential distributional area under each of three assumptions regarding dispersal ability. An unrealistic assumption was that species could disperse to any site at which conditions were favourable for population persistence ('universal dispersal'), that is, raw, uncut distributions were compared before and after change. More realistic was the assumption that species would be able to disperse through continuous habitat but not jump over barriers ('contiguous dispersal'), that is, the modelled actual distribution was overlapped with the post-change prediction, and areas of continuous habitable environments that touch the present distribution were identified; discontinuities of one pixel or greater (~4 km) were considered barriers to dispersal. Another more realistic assumption was that species were simply unable to disperse and would inhabit only those portions of present distributional areas that remain habitable ('no dispersal'), that is, the modelled actual distribution was reduced to those areas predicted to be habitable post-change. These analyses assume no evolution in niche characteristics<sup>21</sup>, and do not take into account interactions among species such as competition, predation, and so on.

## Community turnover

Each species was predicted to experience local extinction and colonization, depending on the climate-change scenario and dispersal assumptions. To evaluate geographic patterns in these shifts, under the contiguous areas dispersal assumption, we summed local extirpations (*E*) and local colonizations (*C*) separately across all species, and averaged the summed maps under the two climate-change scenarios. In this way, we summed distributional shifts across the entire fauna. We added present distributions across all species to create a map of current species richness (*S*), and calculated expected percentage species turnover as  $100(E + C)/(S + C)$ .

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Correspondence and requests for materials should be addressed to A.T.P. (e-mail: town@ukans.edu).

**Extraction of a weak climatic signal by an ecosystem**

Arnold H. Taylor\*†, J. Icarus Allen\* & Paul A. Clark‡

\* Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, UK

† Department of Mathematics and Statistics, University of Plymouth, Plymouth, UK

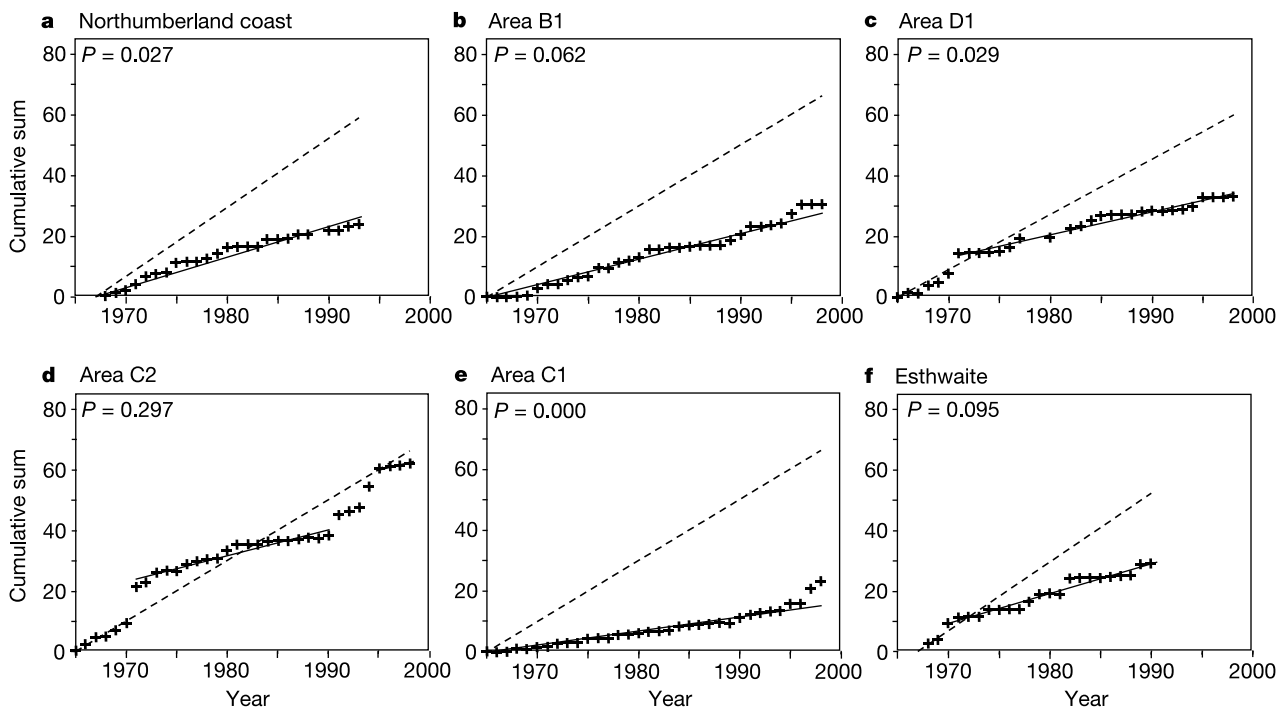
‡ Department of Geography, University of Sussex, Brighton BN1 9SJ, UK

The complexity of ecosystems can cause subtle<sup>1</sup> and chaotic responses to changes in external forcing<sup>2</sup>. Although ecosystems may not normally behave chaotically<sup>3</sup>, sensitivity to external influences associated with nonlinearity can lead to amplification of climatic signals. Strong correlations between an El Niño index and rainfall and maize yield in Zimbabwe have been demonstrated<sup>4</sup>; the correlation with maize yield was stronger than that

with rainfall. A second example is the 100,000-year ice-age cycle, which may arise from a weak cycle in radiation through its influence on the concentration of atmospheric CO<sub>2</sub> (ref. 5). Such integration of a weak climatic signal has yet to be demonstrated in a realistic theoretical system. Here we use a particular climatic phenomenon—the observed association between plankton populations around the UK and the position of the Gulf Stream<sup>6,7</sup>—as a probe to demonstrate how a detailed marine ecosystem model extracts a weak signal that is spread across different meteorological variables. Biological systems may therefore respond to climatic signals other than those that dominate the driving variables.

Figure 1 illustrates this relationship with the latitude of the Gulf Stream (the GSNW index<sup>6,7</sup>) at five locations in the North Sea over a period of three decades using zooplankton data collected by the Continuous Plankton Recorder Survey<sup>8</sup>, together with zooplankton data from a site off the Northumberland coast<sup>9</sup>. These are expressed as cumulative sums of the square of the difference between the zooplankton and GSNW index series after each series has been converted to a mean of zero and unit standard deviation<sup>10</sup>. Cumulative sums provide a sensitive test of whether the relationship is constant with time. When the variables are positively correlated the slope of the graph will be close to zero, rising to 2.0 if the variables are uncorrelated. In the central and southern North Sea abrupt changes in slope show that the relationship has not been constant with time. Figure 1 also shows data for a freshwater lake in the north of England, Esthwaite water<sup>11</sup>, and similar results have been obtained in a neighbouring lake, Windermere<sup>12</sup>. The probabilities that slopes such as these might arise by chance (see Methods section) are also shown in Fig. 1. Similar probabilities calculated using the North Atlantic Oscillation (NAO) index<sup>13</sup> instead of the GSNW index were much higher and all were over 0.1, showing that the GSNW teleconnection is distinct from the effects of the NAO.

In order to determine how the GSNW signal finds its way into the plankton, time series of hourly surface heat fluxes calculated from



**Figure 1** Correlation of observed plankton populations in and around the UK with the latitude of the Gulf Stream. Cumulative sum of the square of the difference between the abundance of total copepods and the GSNW index (crosses) at a site off the coast of Northumberland; in northern (B1), central (C1 and C2) and southern (D1) areas of the

North Sea and in Esthwaite water, UK (using *Daphnia* instead of total copepods). The solid lines are regression fits (included only to highlight the linear parts) and the broken lines show the results for an uncorrelated pair of time-series. The probabilities *P* that the slopes arose by chance are shown.